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ON THE ORIENTATION OF SEA FANS (GENUS *GORGONIA*)

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Sea fans (*Gorgonia ventalina* and *G. flabellum*) grow in patches at depths of 2 to 10 m on the seaward reefs of the Florida Keys. The sea fans in any particular patch appear to have a preferred orientation of their fan "blades." Théodor and Denizot (1965) have noted this phenomenon and concluded from the parallel orientation of algae and gorgonians that the orientation of all fan-shaped sessile organisms is perpendicular to wave motion and that it may result solely from hydrodynamic phenomena. We have asked the questions, "To what extent do sea fans on Florida reefs show preferred orientation?" and "What can be inferred from the morphology of the sea fan and from the habitat concerning the mechanism that brings about this orientation?"

Methods

We worked on several coral reef sites on the upper Florida Keys over July and August, 1966, and put in more than 25 man-hours making observations and photographs while using self-contained underwater breathing apparatus. We spent at least one fifth of this time diving through twilight hours and into darkness. We exposed twenty-four 50-foot rolls of Super 8 mm movie film using a Kodak M-6 camera with close-up lenses to record observations and to aid further study of the activities of soft and stony corals.

For measurement of the orientation of sea fan blades to points of the compass, a waterproof compass was mounted in the center of a 12″ square white plastic board. Holding the board horizontally we then placed a side of the board flat against the blade of a sea fan and made a pencil mark on the board at the north arrow. We measured maximum height and breadth of the fan to ± 0.5 cm with a 30 cm rule and recorded these figures next to the orientation mark. We recorded these data for every fan in each patch studied. We surveyed patches in the following places:

1. Carysfort Reef, 3 to 5 m deep, 48 fans.
2. Carysfort Reef, 1 to 2 m deep, 24 fans.
3. Carysfort Reef, 7 to 9 m deep, 49 fans.
4. Key Largo Dry Rocks, 3 to 5 m deep, 26 fans.
5. Conch Reef, 4 m deep, 27 fans.

We computed the mean angular orientation of all fans in each patch and the deviation in degrees of each fan from the mean orientation of its patch. The deviations are plotted against fan height in Figure 1.

After taking the orientation data, we collected several large fans from Conch Reef and cut a transverse slice 2 mm thick from the stem of each fan between the blade and the holdfast. We then traced the outline of the slice and the pattern of concentric growth rings and centers of growth in the axial skeleton with the aid of a camera lucida attachment to a Wild M-5 Stereomicroscope. To each such tracing (Fig. 2) we added a line indicating the plane of the fan at the time it was collected.

Shear modulus of elasticity of the axial skeleton was measured in thick basal pieces and in pieces of the web of the fan. This was done by hanging weights on excised and horizontally supported skeletal fragments and measuring shear displacement at various stresses with a vernier caliper.

Results and Conclusions

Figure 1 is a graph showing each fan recorded according to its maximum height (abscissa) and the orientation of its blade with respect to the other fans in its patch (ordinate). All fans from all five patches are shown. If all fans in a patch were perfectly parallel to one another, the points would lie along the abscissa. If the fans were randomly oriented, the points would be randomly distributed over the graph. Reasons for paucity of fans less than 20 cm tall are not clear. Small fans are difficult to find among the abundant plants and animals in that size range. We conclude that the smallest fans are randomly oriented and that there is an increased degree of preferred orientation with increased fan height.

We examined two alternative explanations concerning the mechanism of increasing preferred orientation with increasing size. If fans are oriented to some pattern

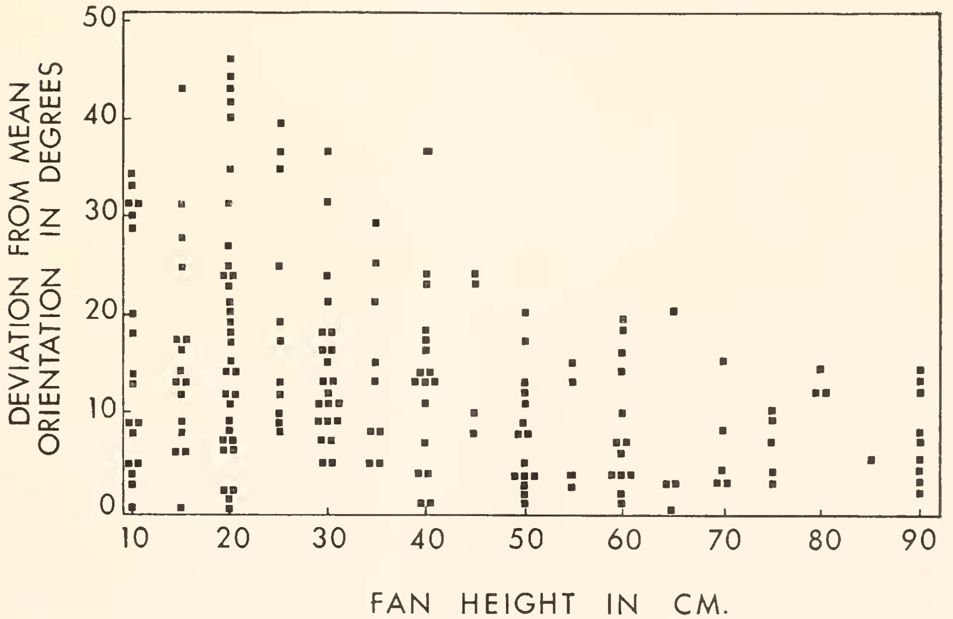

Figure 1. Graph showing the height and orientation of all sea fans in five patches on Florida reefs. Orientation is shown as the deviation of each fan's orientation from the mean orientation in the patch. Since the trend illustrated was shown in each of the five patches, data from the five patches are pooled here.

of water movement, are the fans which are not so aligned destroyed by the water movement, thus selecting only the fans that initially had the preferred orientation for each patch? Alternatively, are randomly oriented fans twisted and held perpendicular to the predominant direction of water movement? The nature of the axial skeleton allows it to "give" or display creep under sustained force, and the subsequent addition of axial skeletal material around the older material would tend to hold each fan in its new orientation.

Transverse sections of the axial skeleton of a sea fan show materials of three different textures: (1) axial centers about 0.2 mm in diameter that are not obviously layered and tend to be colorless and transparent; (2) axial medulla, the cola-colored fibrous material (gorgonin) that makes up the bulk of gorgonian axial skeleton, formed into cylinders around axial centers; (3) axial cortex of coarse gorgonin that surrounds the axial medullae in the bases of large fans and that is the mechanically dominant component of the holdfast (Fig. 2).

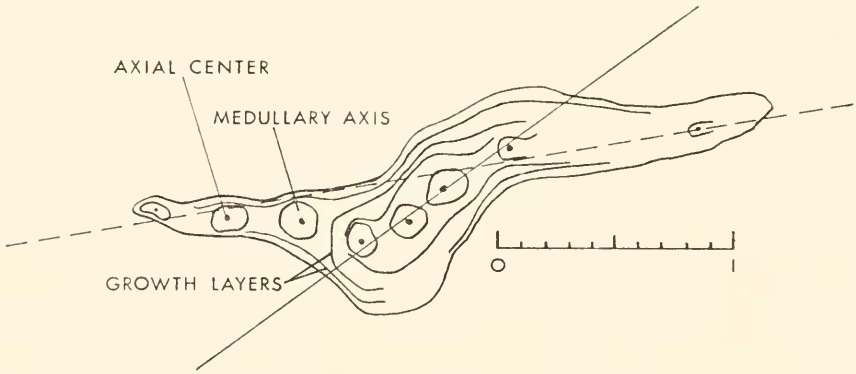

FIGURE 2. Cross-section of the axial skeleton of the stem of a sea fan traced with the aid of a camera lucida. Dashed line: the plane of the fan blade when it was collected. Solid line: possible earlier orientation of fan blade. The number of growth layers indicate the relative age of the axial material: the innermost layers are the oldest. Scale: 1 cm.

The relative age of axial centers can be inferred from the number of layers of axial cortex surrounding each center: the more layers of cortex, the older the center. The alignment of the oldest two or three centers is inferred to be the alignment of the fan at an early stage. The alignment of the outermost (youngest) centers is. we find, the alignment of the fan at the time the fan was collected. In many large fans the early alignment of the blade is seen to be different from the final alignment, indicating a change in orientation of the blade concomitant with growth in height of the blade. We conclude that the orientation of sea fans on shoal Florida reefs can change in time with the growth of the fan.

The fan blade is supported by a few thick axes radiating from the center of the lower edge of the blade and by the even web of axial skeleton of the blade. The axis of the web consists almost entirely of axial center material and has a low shear modulus of 1.22×10^9 dynes cm^{-2} and can undergo extreme lateral deformation: it can be bent double in a distance of 3 to 4 cm without fracturing. The thick basal axis, composed mostly of gorgonin, has a higher elastic modulus, 2.34×10^{10} dynes

cm^{-2}, and cannot withstand great deformations. This accounts for the shape taken by fans as they are bent by waves: the basal portion bends very little but the lower modulus, highly deformable upper part is bent to a position parallel to the direction of wave motion. Thus the parts of the fan farthest from the reef surface meet the maximum current velocities (see Discussion, part I) and are the very parts that offer least elastic resistance to the current. Since the current velocity is greater farther from the reef surface, the effect of this orienting force is greater on the larger fans.

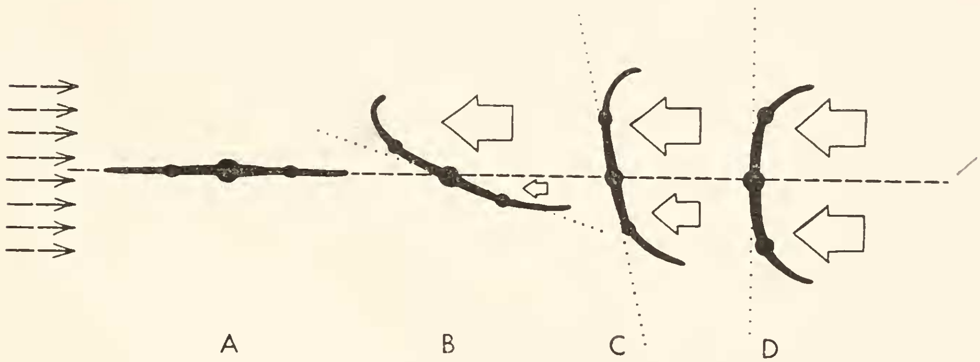

FIGURE 3. Diagram of the orientation of a sea fan (or of any flat, flexible object attached by a stem continuous with a midrib) to the direction of an impinging current as seen from above. Dashed arrows and line: direction of flow. Dotted line: orientation of the fan blade in the absence of current. Outlined arrows: relative magnitude of the forces exerted against the current by leading and trailing edges of the fan blade. A: fan blade parallel (0°) to current and showing no twist. B: fan blade at low angle to the current and showing maximum twist being applied to the stem. C: fan blade at larger angle to the current and showing low twist. D: fan blade perpendicular to the current, also showing no twist.

DISCUSSION

It is highly probable that water movements are the dominant cause of the oriented growth of sea fans. Théodor and Denizot (1965) state that mechanical stability of flexible planar organisms such as sea fans is realized only when the plane of the fan is perpendicular to the direction of impinging water movements. They also state that any twisting of the bases of sessile foliaceous organisms that result from nonperpendicular orientation would decrease their resistance to fracture. By way of partial explanation of why either of these statements should be true, we present the following points of discussion.

I. *Current patterns and fan size orientation.* The velocity of water flowing over a reef varies from zero in the boundary layer within a millimeter of the reef surface to a maximum a meter or so from the reef surface. Coral heads, algae, gorgonians, *etc.*, that project from the reef into the current alter the velocity and direction of flow and create a region of minimum velocity over the reef among these obstacles. These same irregularities will disrupt any laminar tendency in the flow within the region of minimum velocity from that of any prevailing current to a complex turbulent pattern with localized components going in many directions. Small fans growing completely within the region of low velocity could therefore be expected to have random orientation with respect to a prevailing current direction over the reef. As a fan grows out of the turbulent, low-velocity region so that its blade extends into the prevailing current, the current that impinges on these taller fans approaches laminar flow in a predominant direction. These observations are consistent with (1) the observed random orientation of small fans and the preferred orientation of large fans, and (2) the hypothesis that water movements control the orientation of sea fans on the reef.

II. *Current direction and sea fan shape.* The average sea fan is a blade with one or more vertical or nearly vertical, thickened axial supports that extend from the holdfast to the blade and through most of the height of the blade. It is important to note that the blade is almost uniform in thickness and is flexible throughout, while the axial support, being much thicker at the base and tapering from the holdfast to the top of the blade, is stiffer than the blade. A model of this arrangement of blade and axial support can readily be made of plastic. Such a model or a real fan can be moved through water thus simulating flow past a stationary fan while the stem is held by hand.

When the model or a fan is so held and so moved, there are three conditions that are notable (Fig. 3). First, when the blade is exactly parallel (0°) to the direction of flow, and second, when it is perpendicular (90°) to the flow: no twisting moment can be felt in the stem. And third, at any other angle of the blade to the water movement, a twisting moment occurs that is strongest at angles near 0° and decreases as the angle increases to 90°. It is readily seen that at low angles to the direction of flow the leading edge of the fan is bent strongly to one side, thus exposing to the current a surface of almost half the fan (Fig. 3B). This current impinges on the area of the fan perpendicular to the current and produces a large twisting moment. At angles approaching 90°, the trailing edge of the blade presents an increasing area to the impinging current until, at 90°, the forces on both sides of the axial support are equal and there is no twisting moment and hence maximum positional stability.

(1) The shapes that fans take when they are oriented at different angles to the current, (2) the resulting twisting moments and the ability of the fan's supportive system to twist with this moment, and (3) the growth of the axial skeleton by the addition of peripheral layers lead us to suggest that the high degree of preferred orientation observed among large fans in a patch comes about by the fans' being passively twisted and held by the current during periods of growth of the axial skeleton. In this matter, we agree with Théodor and Denizot (1965): we have attempted to explain the phenomenon.

III. *Why sea fans are not parallel to the current.* It remains to explain why, in any patch of fans, one doesn't find half the fans oriented parallel to prevailing currents and the other half oriented at right angles. In a current, small deviations of blade orientation from 90° to the current produce small twisting moments, whereas small deviations from the parallel orientation produce much greater twisting moments. Since sea currents do not hold their directions precisely for long periods of time (see part IV), deviations would be the rule and fans oriented initially parallel to the prevailing current would be subjected to the greatest twisting moments and therefore the greatest tendency to be re-oriented to the stable perpendicular position. We therefore conclude that the direction of preferred orientation of fans in a patch must be perpendicular to the prevailing current.

IV. *Possible stimuli to periodic variations in growth.* The aspect of the subject of sea fans and their habitat that we know least about is the identity and direction of the currents and the time over which they act. *A*. The Gulf Stream sweeps coastal waters northeasterly, parallel to the reef front, during summer months when the prevailing winds are onshore, keeping the Gulf Stream close to the Keys. During winter months prevailing winds are offshore causing the Gulf Stream to move offshore and allowing eddy currents flowing southwest to dominate the water movements over the reefs. These currents are the slowest with the longest period (*ca.* 6 months). *B*. Tidal currents that flow in and out of Florida Bay through the channels between the Keys may provide any directionality according to the position of the reef in question relative to these channels. Close to the channels, the tidal currents will be generally perpendicular to the reef and considerably faster than the currents described in *A*. Their period is a few hours. *C*. Wind-driven surf and surge may come from any direction and have no set period. Direct observations while diving and study of movies show fans on the reef to be constantly waving to and fro with a period of a few seconds. It seems likely to us that some mean direction of all these currents over a full year may be important to the fans. However, we feel that the more violent surf and surge are very likely the most important component in the orientation of sea fans. The short period and alternation of current direction by 180° could provide continuous and constantly renewed directional stimuli to the skeletogenic system of the fan.

Since the axial skeleton of sea fans is a composite material of calcite, fibrous gorgonin containing a collagen-like component (Marks *et al.,* 1949) and probably supplemented by soluble organic matter, it might be expected to share some of the growth-controlling factors with other known composite materials such as bone (Becker *et al.,* 1964) and wood (Kennedy and Farrar, 1965). All these materials have piezoelectric properties and semiconductor properties that can provide electric stimuli to cells in their immediate vicinity. The formative processes of these materials respond to daily, seasonal and annual variations in mechanical stress stimuli by selectively varying the rates of synthesis of the components of the composite material. Experimentally varied mechanical stimuli have been shown to cause variations in growth rates of components in wood (Kennedy and Farrar, 1965) and in insect cuticle (Neville, 1963). Mollusc shells (Barker, 1965) and the skeletons of stony corals (Wells, 1963) show "growth rings" that may represent tidal, daily, lunar, seasonal and annual periods, though experimental evidence for this correlation is lacking. Our own observations of *ca.* 10-μ growth increments in sections 10 to 50 μ thick of axial skeletons of sea fans and other gorgonians lead us to propose a similar mechanism for these organisms: the mechanical stimuli of the waves of surf and surge could be transduced to electrical phenomena by the composite material in the skeleton. These electrical phenomena may then stimulate or inhibit the various synthetic activities of the adjacent skeletogenic cells. The relatively high frequency of this category of water movements renders it subjectively important as a major skeletogenic stimulus.

V. *Mechanical properties of soft vs. stony coral skeletons.* In areas of the sea where water movements have a prevailing direction, many kinds of sessile organisms grow oriented to the prevailing current direction (*e.g.,* Heezen *et al.,* 1966; Riedl, 1966; Théodor and Denizot, 1965; Riedl and Forstner, 1968). Coral reefs abound with sessile organisms and many of them are known to be thus oriented. On Caribbean reefs the species with the most striking degree of preferred orientation is the elkhorn coral, *Acropora palmata,* which has two modes of preferred orientation (Shinn, 1966) : one is a flattening of the colony shape that is inversely related to depth and the other is an orientation of branches parallel to prevailing water movements. Since *Acropora palmata* and *Gorgonia flabellum* occur together on many reefs, it is of interest to examine the fact that the sea fan presents its maximum area perpendicular to the prevailing current while the stony elkhorn coral presents its minimum area to the current.

A major function of skeletons is that of support. This is true in plants and animals alike. In general, all solid, nonhydrostatic skeletons can be described as we have in part IV as composite materials (Slayter, 1962). This statement implies that in each supportive structure there are at least two kinds of material: one of high tensile strength and high elastic modulus that lends these properties to the whole structure, and the other a softer, weaker, low modulus material dispersed among units of the first. This softer material serves to dissipate shock stresses concentrated by the more brittle material and imparts viscous properties to the structure.

Solid skeletons can be separated into two categories: those whose largest volume fraction is a mineral (bone, mollusc shell), and those with little or no mineral (wood, insect cuticle, vertebrate tendon). Although the skeletons of *Acropora* and *Gorgonia* have not themselves been analyzed in detail, information on skeletons of related genera is available. The skeleton of stony corals is known to be mainly aragonite and to contain less than 5% by weight of organic matter (Silliman, 1846). In *Pocillopora,* for example, the only insoluble organic material isolated from growing branch tips is chitin in submicroscopic fibrils, oriented randomly within each tangential growth increment (Wainwright, 1963).

The axial skeleton of the gorgonian *Leptogorgia* when dried under tension yields wide angle x-ray diffraction patterns characteristic of collagen (Marks *et al.,* 1949). Sections cut for the present study from the basal axial skeleton of *Gorgonia flabellum* show strong positive axial birefringence throughout most the thickness of each concentric growth increment and a thin, irregularly birefringent component with an axis of preferred orientation which varies around a plane perpendicular to the axis. The small amount of calcite present may or may not be entirely accounted for by the occasional inclusion of mesodermal spicules into the axial substance.

These brief descriptions of the skeletal textures of stony corals and gorgonians can be correlated with what little we know of their mechanical properties. Scleractinian skeleton is rigid and brittle, and any such skeleton found in an area of surf or surge is either massive or encrusting in such a form that compression forces impinging on the coral are effectively withstood. Branches of *Acropora palmata* break cleanly when hit with a hammer. Gorgonians in general and *Gorgonia* in particular are remarkably flexible and exceedingly strong in shear and tension. To remove a large one from the reef, it is easier by far to hack away the reef limestone around the base of it, than to try to break or cut through the basal axial skeleton. Sea fans and other gorgonians can undergo very large deformations in bending, but although they are elastic they are not completely so and unless some restoring force is applied to them, the skeleton will creep and show permanent deformation or at least very long retardation spectra.

Two very different types of supportive systems have evolved that allow both soft and stony corals to grow on surf-beaten coral reefs: (1) Rigid, brittle, highly mineralized stony corals either build massive structures that take waves as compressive forces and if they are branched, they present their smallest projected area to the current. And (2) the supple, highly deformable but visco-elastic, fibrous gorgonians simply bend with the current and, if they are flat, they become effectively oriented to expose their maximum area to the direction of the current. When the current is fast it merely bends them and has not the force either to break their stems or to dislodge their holdfasts from the reef. Since wave action is to and fro by nature, gorgonians are seldom deformed by creep in the skeletal material in response to a unilateral force (Théodor, 1963) but are, in calm moments, seen to stand straight up.

VI. *Trophic adaptations and coral shape.* Laborel (1960) said that the orientation of sessile marine animals is due in part to hydrodynamic factors and is suited to the nutritional mode of each species. Although he was not concerned with hermatypic organisms, he assumed gorgonians fed on particulate organic matter suspended in the sea water. He hypothesized that fan-shaped animal colonies could best collect their food if they were oriented perpendicular to the predominant current. Théodor and Denizot (1965) noticed that all foliaceous animals and algae on horizontal substrata tend to be oriented perpendicularly to wave motion, and since they found no correlation between the incident direction of sunlight and the orientation of foliaceous algae, they discounted the importance of the nutritional mode of any organism in determining its orientation.

We have made concerted efforts to observe and photograph feeding by soft and stony hermatypic corals and to observe the microhabitat around the coral polyps from which they must take nutrient materials. Few gorgonians have been seen on coral reefs actually feeding (Wainwright, 1968), and the known rates of photosynthesis for hermatypic gorgonians are high enough to allow the hypothesis that photosynthesis is their chief mode of nutrition (Kanwisher and Wainwright, 1967). Unpublished observations of feeding activities of stony coral polyps in the field and in the laboratory over ten years and three oceans convince the senior author that the catching of a suspended food particle by a coral polyp of a few millimeters' diameter is not effected simply by erecting the responsive polyp into the main current. We therefore agree with Laborel (1960) in that the hydrodynamic situation at this level is insufficiently known to allow conclusions concerning the relationship of modes of nutrition to patterns of growth and orientation of fan-shaped gorgonians.

Working with pinnately branched hydroids, Riedl and Forstner (1968) have recently reported high correlations among the following: orientation of the colony perpendicular to the direction of current, the bending of the colony, its branches and polyps, and the rate of flow at the point where polyps are actually catching zooplankton. They measured flow rates in the immediate vicinity of the polyps with a minute bead thermistor. Theirs is the first quantitative information we have on the subject, and it is consistent with the hypothesis that orientation of fan-shaped organisms is controlled by hydrodynamic forces. Their information also strongly suggests what we have suspected, namely that the pattern of flow around feeding polyps is under partial control of the size, shape, orientation and physical properties of the colony's support. An extension of this idea is that the polyps' ability to catch zooplankton will depend on these same features of its supportive system.

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Summary

1. Measurements were made of the orientation to points of the compass of the plane of 189 sea fans from five patches on shoal reefs in the upper Florida Keys. Small fans were observed to be randomly oriented, whereas large fans showed a high degree of preferred orientation within each patch. Microscopic examination of the axial skeleton of some large fans revealed progressive changes in orientation that had taken place during growth. A passive mechanism of orientation is suggested. Due to the high velocity and short period of surf and surge and the observed motions of fans on the reef, surf and surge are judged to be the most important components of water movements controlling fan orientation.

2. Colonial cnidarians have evolved two different composite systems of effective support against surge on the shoal reefs. (a) Branched stony corals have rigid, highly mineralized skeletons that present their smallest projected area to the current. (b) Alcyonarian (soft) corals have highly deformable, fibrous-organic axial skeletons that expose maximum area to the current.

3. We are just beginning to understand the relationships between biological building materials and the functional supportive systems in which they are found.

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